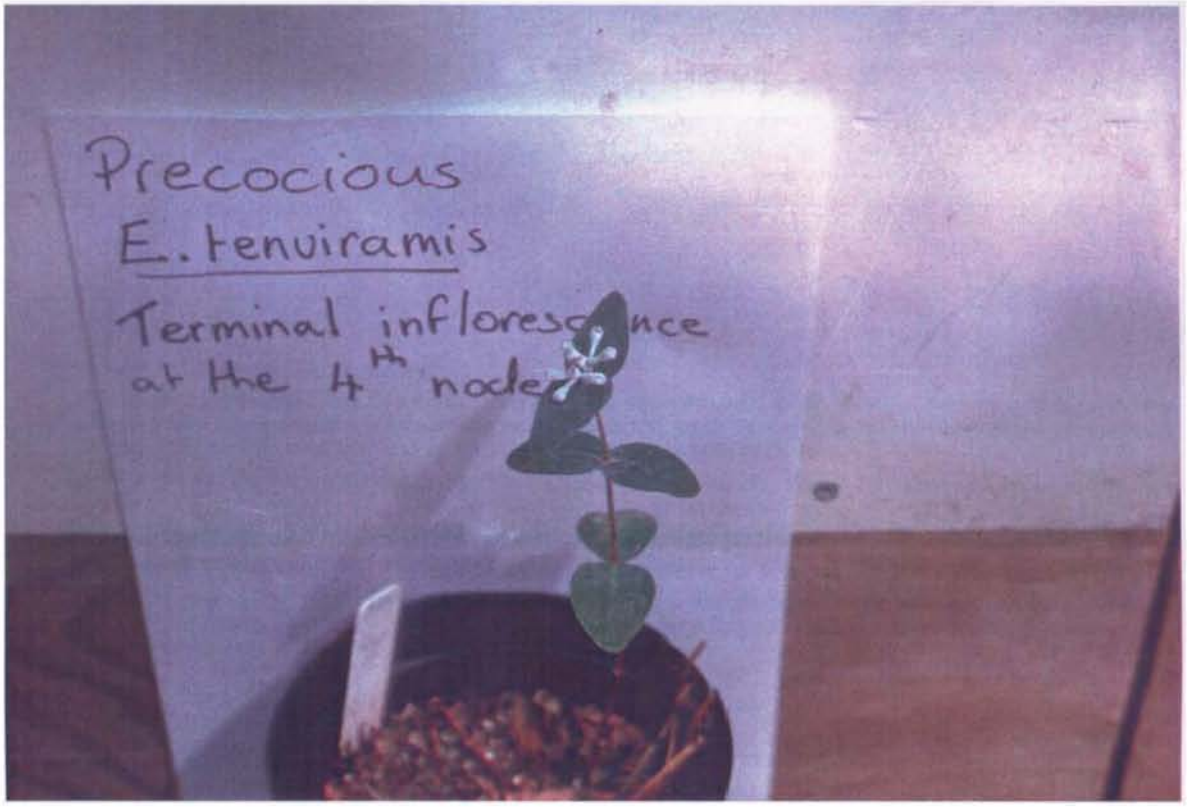

Precocious
E. tenuiramis
Terminal inflorescence
at the 4th node

"Progenesis"

HETEROCHRONY AND HETEROBLASTY IN THE *EUCALYPTUS RISDONII* HOOK.F./ *E. TENUIRAMIS* MIQ. COMPLEX.

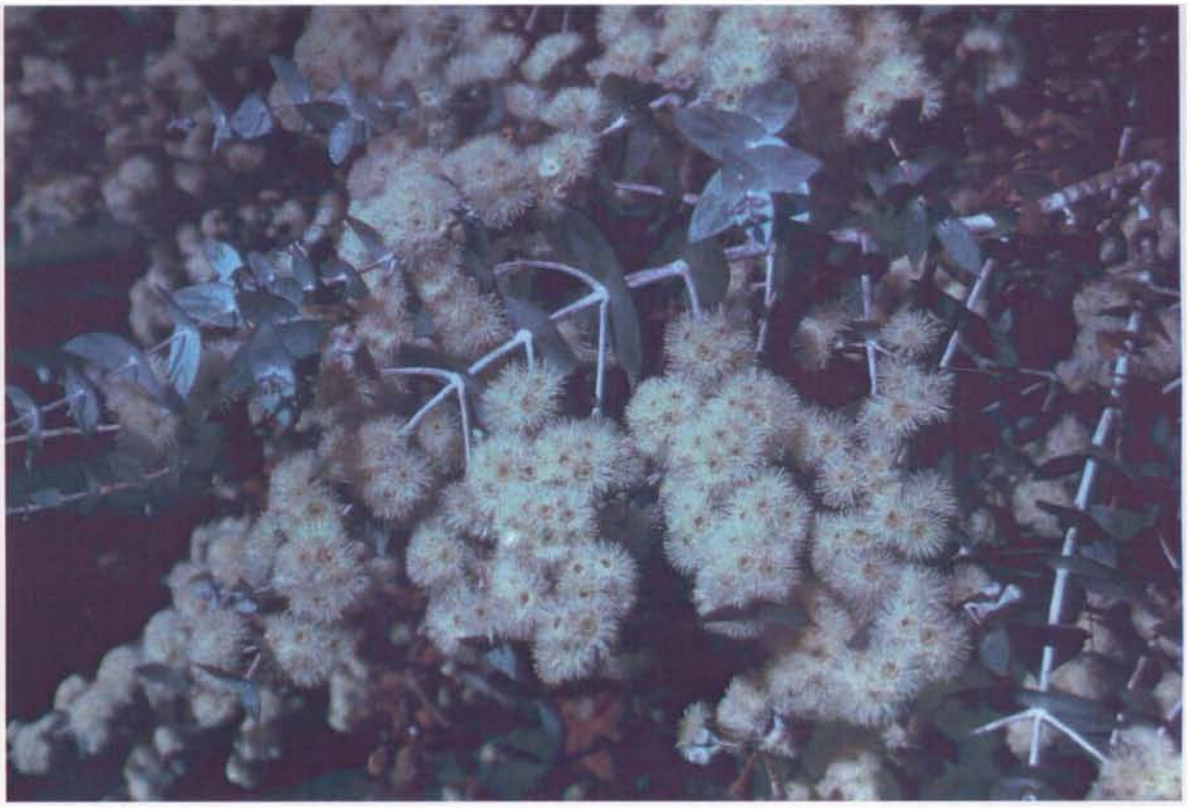
Robert J. E. Wiltshire

submitted in fulfilment of the requirements for the

Degree of Doctor of Philosophy (Botany),

University of Tasmania,

1991.



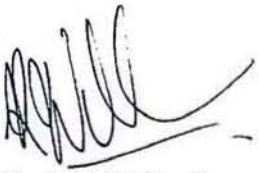
"Neoteny"

At one time I thought that the narrow-leaved forms of E. Risdonii *(var.* elata *and var.* hypericifolia*) could be combined as one narrow-leaved form, but Rodway, at page 368 of his 1910 paper, shows that this cannot be safely done in the present state of our knowledge. Some day a leisured Tasmanian botanist, with adequate field and horticultural opportunities, may collect large series of specimens, connect them with their seedlings in all stages, and work out the phylogeny of this interesting little group.*

(J. H. Maiden 1918)

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and contains no copy or paraphrase of material previously published or written by another person, except where due reference is made in the text.



R. J. E. Wiltshire

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But most of all, I owe a debt of gratitude too large to be repaid to my family, whose love and support made this self-indulgence possible.

Contents

Abstract

Ontogenetic and morphological variation in 40 populations of the closely related species, *Eucalyptus risdonii* Hook.f. (Risdon Peppermint) and *E. tenuiramis* Miq. (Silver Peppermint), was assessed in a multivariate study of heteroblastic leaf (adult and juvenile) and fruit characters. Present taxonomic treatment of the two taxa is based on ontogenetic differences but this study reveals that the variation in the retention of the juvenile leaf habit is continuous. The morphological data suggests that at least four phenetic groups exist in the *E. risdonii/tenuiramis* complex and that, when ontogenetic variation is removed, the morphological variation between some *E. risdonii* and some *E. tenuiramis* populations is continuous and much smaller than the morphological differences within *E. tenuiramis*. An extensive progeny trial, undertaken to remove the confounding effects of environmental and ontogenetic variation, revealed that the genetically-based variation between geographically contiguous populations of *E. risdonii* and *E. tenuiramis* is relatively small and appears to be continuous. Reliable classification into either taxon, on the basis of seedling phenotype, is not possible for this group of populations. The major dichotomy between phenetic clusters derived from the seedling morphology is not between forms that can be assigned to *E. risdonii* and *E. tenuiramis*, but between geographically isolated forms of *E. tenuiramis*. This disjunction in phenetic distance between the Central East Coast populations and the remaining *E. risdonii/tenuiramis* populations parallels the geographic disjunction between the two that has existed since at least the last glaciation. The combination of clinal variation between contiguous *E. risdonii* and *E. tenuiramis* populations and the divergence of the isolated East Coast phenotype suggests that both ecological separation and reproductive isolation may be necessary for speciation to occur in the eucalypts, especially in a climatically unstable environment such as Tasmania.

Phenotypic variation in ontogeny between forms classified as *E. risdonii* and *E. tenuiramis* has been shown to be genetically based. When grown in a common garden environment to 10 years of age, all progeny from the *E. tenuiramis* type mothers had attained the petiolate leaf condition, whereas most progeny from the *E. risdonii* type mothers still retained the connate, juvenile leaf type. Progeny from intermediate mothers displayed a large variation in the height of phase change but could be regarded as intermediate. This suggests that there is a cline in the retention of the juvenile leaf form (neoteny) in the *E. risdonii/tenuiramis* complex. The time to reproductive maturity and subsequent reproductive loads have also been shown to differ markedly between the two forms. The *E. risdonii* progeny became reproductive much earlier than the *E. tenuiramis* progeny, and bore a heavier reproductive load. This precocious attainment of reproductive maturity can be regarded as progenesis. Both changes in developmental timing (heterochrony), may lead to paedomorphy but in response to different selective forces. Neoteny is probably a response to drought, whereas progenesis appears to be a response to frequent disturbance.

Studies of the anatomy and photosynthetic response of the juvenile and adult leaf phases of one of the *E. tenuiramis* phenotypes indicates that heteroblasty in the complex is not a response to regeneration under mesic, low-light conditions as it appears to be in wet sclerophyll species. In spite of a leaf arrangement that favours maximum light interception, the juvenile leaf phase appears to be adapted for droughted, high light intensity conditions. These xeromorphic adaptations reach their greatest expression in the Government Hills *E. risdonii* phenotype, which supports the contention that retention of the juvenile leaf morphology conveys significant selective advantages in these water limited habitats.

The effect of photoperiod and temperature on the transition from the juvenile to the adult leaf phase was examined in *E. tenuiramis*. The results from the first trial suggest that photoperiod does not affect phase change since no differences were observed between treatments in chronological time, nor number of nodes, taken to reach phase change. A second trial, conducted under higher temperature and light intensity conditions, emphasized the reliability of physiological time (as measured by node number), rather than height or chronological time, as an index of ontogenetic development in *E. tenuiramis*.

The nature of this rigid physiological control of phase change was examined at the individual plant level, revealing interesting differences between the positional control of phase change in lateral branches and epicormic shoots. A model is proposed that describes how many nodes an epicormic shoot will require to attain phase change from any given position in the plant. Two theories are proposed to account for the behaviour of the epicormic shoots, one involves a gradient in juvenility within the plant, whereas the other suggests that accessory buds 'remember' their position but are altered by the length of their suppression. Further experiments are described that attempt to resolve this question. The results indicate that the control of phase change is inherent in the apex and that it is relatively independent of gross changes to its hormonal and nutritive environment, although it can be affected by the length of its suppression.

This study of the variation in the *E. risdonii/tenuiramis* complex has illustrated that heterochrony is a powerful means of altering morphology with only minor changes to the genome. These large differences in the adult phenotype have led to the classification of the two forms into distinct species, yet this does not appear to be an accurate reflection of the genetic distance (nor, consequently, the taxonomic distance) between the forms. In this example, speciation by paedomorphy has not been completed. However, many species of eucalypt appear to have arisen by this means and these species are often found in extreme environments. Examination of these taxa indicates that paedomorphy has operated at all phylogenetic levels: operating at present,

within species in a clinal fashion; operating in the recent past, to produce sister species; and at earlier points in the evolutionary time scale, which has produced groups of paedomorphic species. In addition to paedomorphy, other heterochronic processes (peramorphy) are obviously operating throughout the genus, and this evolutionary shifting of the timing of developmental events has a wider significance in eucalypt evolution. Because of this repeated occurrence and operation at all phylogenetic levels, the role of heterochrony in the genus *Eucalyptus* deserves greater recognition and comprehension.